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FERNS OF THE DISMAL SWAMP, VIRGINIA.

BY WILLIAM PALMER.

The ferns of the Dismal Swamp may be divided into three distinct groups according to their place of growth: (1) arboreal species, (2) true swamp species, and (3) ground species. The first group may be divided into two subdivisions: (*a*) those growing on fallen mossy trunks, about the bases of living gum trees, on dead cypress knees, bent gum roots, and on decaying stumps; (*b*) those growing exclusively on trunks and branches of living trees. The first subdivision (*a*) comprises the following species: *Dryopteris marginalis*, *D. spinulosa*, *D. goldieana celsa*, *Polystichum acrostichoides*, *Asplenium platyneuron*, *Struthopteris regalis*, *S. cinnamomea*, *Botrychium obliquum*. The second subdivision (*b*) contains but one species, *Polypodium polypodioides*, which grows exclusively on the trunks and larger branches of living trees, usually high up in the tops, and probably on all the species of deciduous trees. The true swamp ferns include but two species, *Woodwardia virginica* and *W. areolata*, which grow on the peaty remains of former vegetable life, always in wet places and often, especially the former, in water.

The ground ferns occur, not in the true peaty swamp, but in the surrounding low sandy area, which nevertheless constitutes a very large portion of the Dismal Swamp. These are *Dryopteris noveboracensis*, *D. thelypteris*, *Asplenium filixfœmina*, *Pteris aquilina*, *Onoclea sensibilis*, *Struthopteris regalis*, *S. cinnamomea*. But one fern ally (*Selaginella apus*) has been found.

A study of many forms of the life of this vast swamp reveals the interesting fact of the occurrence in abundance of many

southern and northern types. It is a meeting ground where many Austroriparian forms reach their northern limit, while more northern forms either find their lowest or most southern habitat, or have variously changed representatives. The causes of this complex condition vary according to the requirements of the different species and the circumstances of their introduction into the area. In a general way it may be stated that species requiring abundance of sunlight and living above the undergrowth are southern, while those intimately associated with the surface of the swamp are of more northern, or of higher-ground derivation. But there are many exceptions. The swamp undoubtedly has been slowly evolved from a salt-water lagoon to its present condition; hence all its present life has been introduced from surrounding regions.

Of the ferns *Polypodium polypodioides* is distinctly Austroriparian, here reaching almost its northern limit.* *Dryopteris goldieana celsa*, though related to an Alleghenian form, is quite distinct and is undoubtedly its representative. The woodwardias are coastal-swamp species, and though found well into New England do not occur at any great elevation. The two species of *Struthopteris* are most abundant at higher altitudes and owe their presence here to their swamp habits and the ability of the plantlets to find a congenial home. They do not fruit abundantly and doubtless before man interfered with the forest were rare. Seven other species, *Dryopteris marginalis*, *D. noveboracensis*, *D. thelypteris*, *Polystichum acrostichoides*, *Asplenium filixfœmina*, *Pteris aquilina*, *Onoclea sensibilis*, are all higher-ground species. With the exception of *D. marginalis* they are abundant in the general region bordering the swamp. *Botrychium obliquum* also belongs in the same category and may be common about the swamp. Two other species usually found on higher and dryer ground, *Dryopteris spinulosa* and *Asplenium platyneuron*, are not abundant in the swamp, and the former was noticed but once elsewhere. Both are somewhat changed from the typical form, though perhaps hardly sufficiently to warrant separation.

Thus the only species growing on living trees is truly Austroriparian; the next is *D. goldieana celsa*, which occupies a higher habitat in the swamp than any of the others except *D. spinulosa*, which occurs with it, though not so abundantly, and which

* I have taken it near Cape Charles City, Northampton Co., Va.

has also undergone some change on account of its unusual environment.

The flooded condition of the true peaty swamp floor for several months of the year prevents the growth of ground ferns, except the water-loving woodwardias; therefore all the species of the swamp proper which grow near the ground occur just above the high-water line and rarely more than three feet above it.

A systematic examination of the whole swamp for ferns has not been possible, but enough has been learned to show that a number of species have adapted themselves to very unusual conditions, and that some have undergone changes from the normal type. The main factor in determining the character of the pteridophytic life is the flooded condition of the swamp floor for several months annually, but this is less potent now than formerly.

LIST OF SPECIES.

1. Botrychium obliquum Muhl. Oblique Grape Fern.

On June 10, 1899, I found four plants, growing with other species on logs, at the side of Washington ditch. They were sterile fronds of the previous year's growth. The fronds are less ample and the divisions shorter, more rounded and more widely placed than in any specimens from about Washington. The dried roots are stronger, blacker, and more abundant.

2. Struthopteris * regalis (Linn.) Bernh. Royal Fern.

Osmunda regalis Linn., Sp. Pl. p. 1065, 1753.

Abundant, usually in large clumps scattered throughout the swamp and always on dead stumps except in the sandy areas.

In many cases hundreds of dead persistent stipes testify to the great age of the clumps. Just above high-water mark mosses have established a foothold in a broad ring around the old knees of the cypresses, the bends of gum roots, and logs. Various plants, especially ferns, take root in this moss and often reach a large size. The oddity and beauty of such growths are striking, especially on a well-preserved knee where the reddish apex rises several inches above the surrounding moss. (See plate I, Fig. 7.)

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* The ferns usually placed in *Osmunda* evidently belong to Bernhardi's genus *Struthopteris* (not *Struthiopteris* of authors). The essential features of Bernhardi's description are as follows: 21. Struthopteris mihi. *Sporangia* subglobosa, bivalvia. E. g. *Osmunda regalis.* L. — — *Cinnamomea.* L. — — *Claytoniana.* L. * * *. Obs. 2. Caue ne Struthopteridem meam cum Struthiopteride Hall, confundas. (Journ. für die Botanik, Band 2, 126, 1801.)

When little sunlight reaches these plants fruiting spikes are rarely seen, and usually but one on a plant. Along the outlet canal, where the trees have been thinned and drainage is complete, the dryer and more sunny conditions have affected the fruiting and many variations showing partial fertility were collected.

3. Struthopteris cinnamomea (Linn.) Bernh. Cinnamon Fern.

Osmunda cinnamomea Linn., Sp. Pl., p. 1066, 1753.

Abundant, usually with the preceding species, but not so partial to the cypress knees and the shadier situations. Both species, but more especially *S. cinnamomea*, are evidently recent additions to the true swamp flora; far away from the ditches and bogie roads they are rarely seen. This species is usually very tall and luxuriant, but does not fruit as extensively as in more open and higher places. On June 9, 1899, I found two plants near the head of Washington ditch in an open place. They had all the pinnules much reduced in size and many of the lower basal ones were greatly elongated and often pinnatifid. The plants were exposed to generous sunlight for part of the day, but owing to their situation on a decaying log were necessarily limited in root moisture.

4. Onoclea sensibilis Linn. Sensitive Fern.

By no means common in the sandy area but found mainly in the streams and ditches bordering the swamp.

5. Polystichum acrostichoides (Michx.) Schott. Christmas Fern.

On June 3, 1896, several hundred yards from the eastern end of Lake Drummond, I found several dwarfed plants on a small well-decayed log. The largest frond, a fertile one, measured $9\frac{1}{4}$ inches (235 mm.*) and $1\frac{3}{4}$ in. (44) wide, with a stipe $4\frac{7}{8}$ (124) long. The longest pinna is $\frac{7}{8}$ (21.5) long and $\frac{1}{4}$ (5.5) wide. The largest sterile frond was shorter and barely wider. The edges of the pinnæ were regular but very finely spinulose. No others were found, but the species is common in the ravines near Suffolk, about fourteen miles distant.

6. Dryopteris noveboracensis (Linn.) A. Gray. New York Fern.

Where the sandy areas of the swamp blend with the true peaty swamp, and especially in the old bogie roads in these dryer portions of the swamp, this species is abundant.

7. Dryopteris thelypteris (Linn.) A. Gray. Marsh Fern.

Found at but one place, above the head of Washington ditch. Its long spindling fronds were growing in the bushes on the bank, but the normal plant was not seen.

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*All measurements in parentheses are in millimeters.

8. Dryopteris goldieana celsa subsp. nov. Log Fern.

(Pl. I, Figs. 1–6, 8–12.)

Structurally similar to *Dryopteris goldieana goldieana* (Pl. I, Figs. 13, 14), but differing in its very erect habit, longer and narrower fronds with smaller and more widely separated pinnules and pinnæ, and with the apex regularly decreasing instead of crowded and suddenly shortened. Upper basal pinnules of lower pinnæ either absent or very much and usually unequally reduced. Fronds lanceolate or lanceolate oblong. Stipes at base densely covered with large and richly alutaceous scales with brown centers and transparent, sharply defined margins; upper scales paler and almost unicolor. Type No. 340,398 National Herbarium, Dismal Swamp, Norfolk County, Virginia, June 8, 1899, William Palmer (collector's No. 247). Measurement of type, frond 22½ inches (523); longest pinna, the 5th, 5⅜ (136.5); stipe 12 (305). Fertile pinnæ less than 1¼ (31.5) wide; sterile basal pair, greatest width 1¾ (44.5).

Measurements of twenty paratypes: Fronds 10–24 inches (254–609), average 19 (483). Stipes: 7–14½ (178–368.5), average 10½ (267). Largest frond 24 (609.5); stipe 10¼ (261); longest pinna, the 8th, 4⅞ (124; the lowest pinna 4 (101.5). Sterile fronds few, much smaller and less elongate. Three lower pairs of pinnæ of fertile fronds sterile or nearly so.

In habit, situation, and aspect this fern is quite unlike typical *D. goldieana*. It suggests *D. floridana** but differs in outline; its pinnules are not so widely separated, and the shape of the lower pinnæ, especially the two lowest, are quite different, as shown in Figs. 6 and 9–12.

Its relationship to *goldieana* is shown by the character of the scales at the base of the stipe (quite unlike the *cristata* group), by the reduced size of the basal pinnules on the lower pinnæ, the lower one being absent, by the broadest portion of the lower pinnæ not occurring at the base, and by the peculiar stalked character of the rachides of the pinnæ, especially the basal pair. Though occurring in a swamp it is practically a plant of dry habitat, as compared with the broad herbaceous *D. goldieana*, which grows on damp ground. The difference is well shown by comparing the tall and narrow *D. cristata*, characteristic of dryer ground, with the large, coarse *D. cristata clintoniana*, which grows in wetter places. This apparent paradox is rendered plain by the statement that *celsa* does not grow on the ground of the swamp but in moss on stumps and logs where the supply of moisture is limited and where the plants are exposed to a fair, often abundant amount of light. *D. goldieana* grows in damp, rich and well shaded situations. Both these plants are densely covered about the bases of the stipes with large dark brown centered scales, almost black in *goldieana*, most of which are bordered by a narrow, transparent ribbon, the contrast between the two portions being sharply defined.

In *celsa* the rachis is grooved in front even to the apex, but in *goldieana*

**Dryopteris floridana* bears the same relation to *D. cristata*, or rather to *D. c. clintoniana*, that *D. g. celsa* does to *D. goldieana*.

it is stouter, more fleshy and grooved for only a short distance above the lower pinna, or faintly further.

In *D. cristata*, *floridana* and in *clintoniana* the basal pinnules of all the pinnæ are largest and longest; in *celsa* and *goldieana*, some pinnæ, especially the apical ones, are similar, but the lower pinnæ, especially the lowermost, have the pinnules, even for several pairs, very much reduced. In good fertile fronds of *celsa* and *goldieana* the lower basal pinnule of the lowest pair of pinnæ is always absent but sometimes present or apparently present in some undersized fronds. This is often the case in *goldieana*, but only occurs rarely in *celsa*. The basal pinnules of the upper pinnæ of both these ferns are always opposite and very exactly so, but they begin to diverge at the centers of the pinnæ. On the lower pinnæ this pairing is rare and it is not easy to determine whether the opposite of the reduced upper basal pinnule has never been developed or whether it is represented by the one occupying the adjoining position. This latter view would seem to be correct, the lower pinnules having been gradually moved along the rachis toward the tip during the evolution of the form. In very young fronds (Figs. 5, 8) there is a wide space of the lower pinna beneath, the pinnule seems forced away from the rachis and the base of the midvein inclines toward the rachis of the pinna for some distance. The same result is shown in numerous young fronds of both forms. Fig. 14 represents the common type of *goldieana*, while Figs. 6 and 9–12 are from specimens of *celsa*.

Dryopteris goldieana is extremely herbaceous and robust, its pinnules and pinnæ being large and often overlapping. In *celsa* they are always widely separated; both are much narrower, and there is no sudden change from the long, wide pinnæ to the shorter, narrower one of a crowded apex as in *goldieana*. The reduction or absence of the lower pinnules results in producing a stalk for the pinnæ, short in *goldieana*, longer in *celsa*. The pinnæ of *celsa* incline upwards very decidedly, whereas in *goldieana* they stand at a right angle to the rachis or are only slightly inclined upwards. These differences between the very erect narrow *celsa* and the broad, drooping and herbaceous *goldieana* result from differences in habitat, the dryer and lighter situation of *celsa* contrasting in its results with the gloomy, damp habitat of *goldieana*.

On July 30, 1899, I found two clumps of *goldieana* on the Virginia bluffs of the Potomac river opposite Cabin John Bridge. The first contained over fifty plants, all with well drooping fronds and nearly all the lower pinnules of the lower pinnæ normal. These plants were growing at the foot of the talus among the rocks, and the trees formed a dense canopy overhead. In the second clump a mile further down, in a precisely similar situation, were several dozen plants. But here the thinness of the foliage overhead permitted the sun to shine on the plants for several hours daily. The early fronds were drooping as in the first clump, but the later and mostly fertile fronds were more erect, and the divisions were less herbaceous and consequently less crowded, but in no case to the same extent as in *celsa*.

The differences in the character of the lower basal pinnules in these two ferns is ecologically an interesting feature. The usual character of these pinnules in *goldieana* is shown in Fig. 14. In Fig. 13 is shown another, which was growing in bright sunlight, at Great Falls, Virginia; the shortening of the lower pinnules is evident. The first style of frond grows in damp well-shaded situations and droops in such a way that a practically equal amount of light is received by all portions of its upper surface. But a difference occurs when the light is more abundant; then the frond becomes strengthened, that is, more erect, and consequently the upper and middle portions shade the lower pinnæ. A struggle thus ensues between the pinnæ for light. The lowermost, owing to their position, are seriously handicapped, but instead of remaining in the same or nearly the same plane, as in the case of well-shaded fronds, these lower pinnæ turn more toward the light, so that their tips approach each other and their upper surfaces are turned nearly 90 degrees, so as to obtain the light as nearly as possible perpendicular to their plane. In pressing such specimens the stalks of one or more pinnæ are necessarily fractured where they join the stipe. In thus bringing the lower pinnæ almost together in order to obtain the greatest amount of light the greater portion of each pinna is entirely successful, but at the expense of the lower pinnules; especially so on the lowest and less so toward the middle. These lower pinnules are shaded not only by their own overlapping when the pinnæ are flexed, but also by the stout stipe and the pinnules above. Consequently they do not receive a normal amount of light and therefore during the growing period fail to develop perfectly, and are outstripped by the more fortunately placed middle pinnules. One extreme is shown in the usual frond of *goldieana*, the other in nearly every frond of *celsa*. Specimens of *goldieana* collected about Washington, an intermediate locality, altitudinally and geographically, have these basal pinnules in many cases much, and often unequally, reduced, but never to the extent of *celsa*. Similarity of general structure and the ecological character of the differences between these two ferns warrant the view that *celsa* is a true subspecies of *goldieana*, and therefore a geographical race or physiological subspecies. Our swamp plant therefore is a product of abundant light, limited root moisture, and the struggle for existence under peculiar conditions, which do not, or but very slightly, affect its relative.

In June, 1896, near the head of Washington ditch, I found a few immature plants of *celsa* and considered them *D. c. clintoniana*. The following year, at the same place, I found some larger but imperfect fertile fronds. This year, while penetrating the swamp north of the outlet canal and about eight miles east of the other locality, I found numerous plants ranging, through all stages, from those with the first fronds and the remains of the prothalli, to plants over thirty inches high. It is possible that this fern occurs in other localities in the same general region.

The log fern grows in several situations. About the base of a large gum tree, where there was an accumulation of waste woody matter and an

entanglement of various shrubs and other plants, it was abundant and of all sizes. An odd location, and the most common, was along the curved lower side of a fallen mossy trunk where the plants occupied a line just above high-water mark. Usually such a log was exposed to a large amount of light and its upper surface was destitute of mosses and other plants. On other logs usually situated in a tangle and well shaded, the ferns grew in a line along the middle of the top, either with several plants of *D. spinulosa*, a few flowering plants, or more generally alone. In every instance the rhizome was imbedded in the moss and the plants were but loosely attached to the wood; a pull on a frond was generally sufficient to bring up the whole plant.

9. Dryopteris marginalis (Linn.) A. Gray. Marginal Fern.

A most unexpected surprise was the discovery on June 10, 1899, of a single dwarfed plant of this rock-haunting fern. Four miles westward from Lake Drummond up Washington ditch, is a recently made plank road which runs a mile or more into the swamp. Some distance along this road a large tree had fallen years before, and on its broken and decaying stump I found the plant with five fronds, three of which were fertile. The largest measures $8\frac{5}{8}$ inches (219.5), and the stipe $5\frac{5}{8}$ (142.5). The sori are not abundant and are confined to the apex. There are 279 on the best fruiting frond.

10. Dryopteris spinulosa (Retz) Kuntze. Spinulose Fern.

A few large plants were growing on logs with *D. g. celsa* and several immature plants were found near the head of Washington ditch on logs and stumps. They differ from specimens taken about Washington, D. C., in having all the divisions narrower and more widely separated and the apex lengthened. The color is a darker green. The pinnules are more inclined toward the rachis, and the pinnæ trend upward to a greater extent. Some specimens, both large and small, show a more triangular outline, with longer lower pinnæ, and this is evidently the tendency in plants growing in deep shade. In June, 1896, the mouth of a well near Suffolk had many plants growing between the bricks. All were herbaceous and dwarfed, and the single fertile one found had very small sori near the margin.

11. Woodwardia virginica (Linn.) J. E. Smith. Virginia Chain-fern.

Extremely abundant. Its natural habitat is in the pools which occur between the elevations made by the enlarged bases of the trees, and in the cane swamps; but wherever the swamp has been burnt out this fern occurs in greater luxuriance. Along the ten miles of Jericho ditch which has been dug from Lake Drummond through the northern part of the swamp, it is very abundant and large, and grows in the water in dense beds usually for many yards. The fronds are here quite erect and face the sun—*i. e.*, the plane of the frond is at a right angle to the line of aver-

age duration of direct sunlight received by the frond; so that the plants on the east side of the ditch face toward the southwest, while those on the west side approximate the southeast, often to the east, according to the amount of foliage about them. The largest frond collected measures 2 feet 10¼ inches (970), its jet black stipe is 2 feet 9¼ inches long (955) and greatly enlarged at the base. At the outlet canal at the east end of Lake Drummond, where the depth of the canal has drained the adjoining swamp, it is abundant but harsh and less herbaceous, and was found fruiting abundantly in early June. Plantlets were common.

12. Woodwardia areolata (Linn.) Moore. Narrow Chain-fern.

Abundant and growing with its relative except in dryer situations. It is common in low places in the swamp, among the cane and other vegetation and about the bases of the trees. Its delicate fronds grow best where well protected from the sun either by taller vegetation or in wet, densely crowded or well-shaded situations. Prothallium fronds and young plants are numerous on small decaying logs which are well shaded and constantly wet.

13. Asplenium platyneuron (Linn.) Oakes. Ebony Spleenwort.

Near the western end of Washington ditch a dozen or so plants of various sizes were found growing on well-shaded stumps near the water and mixed with numerous other plants. The fronds are all much broader and longer than specimens of similar age from higher and dryer altitudes, and are more deeply and irregularly incised. The pinnæ are wider apart, broader, more blunt, and the basal portion overlaps the rachis. The largest frond measures 18¾ inches long (476), the longest pinna is 1⅝ inches (41.5), and the stipe is $3\frac{7}{16}$ inches (88).

14. Asplenium filixfœmina (Linn.) Bernh. Lady-fern.

Common throughout the sandy woods but not seen in the peaty swamp. A green-stemmed form was the only one found.

15. Pteris aquilina Linn. Bracken.

Seen but sparingly near the upper end of Jericho ditch, where the dredging has formed an embankment.

16. Polypodium polypodioides (Linn.) Hitchcock. Gray Polypody.

Extremely abundant but usually high up in the tree tops. It persists for several years on the fallen trees but finally succumbs. It is abundant on the cypresses standing in Lake Drummond, where its usually dry curled fronds may be reached from a boat. In the woods it is rarely found where it can be easily reached. In the streets of Suffolk it is abundant in wide bands on the trunks of the shade trees, usually growing in dense masses, mostly on the northern sides and about ten feet from the pavement.

EXPLANATION OF PLATE I.

FIGS. 1, 2, 3. *Dryopteris goldieana celsa.* First prothallium fronds, enlarged about twice.

FIG. 4. Second frond of same, natural size.

FIG. 5. Third frond of same, slightly enlarged.

FIG. 8. Fourth frond of same, reduced one-third.

FIGS. 6, 9, 10, 11, 12. Lower basal pinnules of same, reduced one-third.

FIG. 13. *Dryopteris goldieana goldieana.* Lower basal pinnules, from poorly shaded frond, reduced one-third.

FIG. 14. The same, from an ordinary frond.

FIG. 7. Plants growing in moss on a dead cypress knee above high-water mark.

FIGS. 1–5 were drawn from the fronds; Figs. 6 and 8–14 from tracings of photographs, the fronds being used as negatives.